Pacific Science (1989), vol. 43, no. 2

Coral Reef Recovery Subsequent to the Freshwater Kill of 1965 in Kaneohe Bay, Oahu, Hawaii[1]

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ABSTRACT: The reef coral community on the landward side of a patch reef near Kahaluu in Kaneohe Bay, Oahu, Hawaii was resurveyed 18 yr after all live coral was killed by a thick lens of freshwater runoff from a flashflood in 1965. The initial phase of recovery of the reef was documented from 1968 to 1973. A resurvey of the reef was conducted in 1983, using the same methods as the 1973 study. Species, abundance, and distribution of corals on the patch reef were measured and recorded along a series of 10 transects. Results show large increases in size and numbers of colonies, area, and depth range covered by corals. Greatest coral abundance was reported in the upper 5 m, but community diversity did not increase because the fast-growing finger coral, *Porites compressa*, became more dominant. The pattern of coral community succession at this sheltered location was similar to that observed at other environments in the Hawaiian Archipelago. Recovery appears to be rapid in protected, low-wave-energy environments such as Kaneohe Bay, which are infrequently affected by major disturbances. Almost 20 yr after a major disturbance, the Kahaluu patch reef slope coral community is approaching the climax conditions of other reef slope communities in Kaneohe Bay not disturbed by the 1965 flashflood.

CORAL REEF communities are subject to a variety of natural or man-made disturbances (Stoddart 1969*a*, Johannes 1975). Relatively few instances of coral reef recovery have been documented (Endean 1976), especially in the quantitative assessment of coral community dynamics during recovery. Stoddart (1963, 1969*b*, 1974) observed the damage and recovery of British Honduras reefs following cyclone Hattie in 1961. On the Great Barrier Reef, Connell (1973, 1976, 1978) has monitored several permanent meter quadrats on reef flats since 1962. He has reported on their recovery from cyclone damage, but the dynamics of reef flat coral communities may differ from those of reef slopes, where optimum coral development often occurs (Sheppard 1982). The recovery of coral communities on Guam following *Acanthaster* infestations was documented by Randall (1973*a,b,c*). *Acanthaster* destruction of coral reefs and subsequent recovery were broadly investigated by Endean and Stablum (1973*a,b*) and in detail by Pearson (1981). The recovery of coral reef assemblages disrupted by natural disturbances are considered by Loya (1976) to be mainly a function of time. Pearson (1981) defined reef recovery as the restoration of a coral assemblage to a degree comparable to its original state. In reef slope habitats with high coral cover, the recovery process may require several decades following major natural disturbances (Pearson 1981, Sheppard 1982).

In Hawaii, the reestablishment of coral reef communities was studied on submerged lava flows of known age by Grigg and Maragos (1974), who proposed a pattern of long-term

[1] This paper is a product of the 1983 Hawaii Institute of Marine Biology Summer Program in Marine Science sponsored by the Edwin W. Pauley Foundation, the University of Hawaii Foundation, and Sea Grant Program Project No. F 238-F-582-B-315; under grant number NA8IAA-D-00070. Manuscript accepted May 1988.
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succession of coral assemblages in Hawaii. Coral colonization and succession in a newly created harbor habitat were monitored at several times over an 11-yr period at Honokohau, Hawaii (Maragos 1983). In Kaneohe Bay, Oahu, reef slope communities throughout the bay were resurveyed in 1983 to document their recovery 5 to 6 yr after sewage input was diverted to outside the bay (Maragos et al. 1985, Evans et al. 1986).

In the present study, a patch reef at Kahaluu, in Kaneohe Bay, was resurveyed to document coral community composition 18 yr after a freshwater "kill" (see Banner 1968). From 2 to 8 May 1965, Kaneohe Bay watersheds experienced extremely heavy rains and flood conditions. Up to 17.16 in. (43.59 cm) of rain fell in a single day and many streams equaled or exceeded previous maximum heights and discharge rates (Banner 1968). The runoff resulted in a freshwater layer, which formed over more dense marine waters and coincided with very low tides, subjecting nearshore coral communities to considerable salinity stress. General surveys showed coral kills to depths of 5 ft on the inshore reefs in the central sector of the bay (Banner 1968).

The reef slope on the landward-facing portions of a patch reef near Kahaluu Stream was completely denuded of living coral (Banner 1968). It is thought that floodwaters entering the embayment fronting Kahaluu Stream, which is constricted by fringing reef on either side, were blocked by the patch reef (Figure 1). This trapped the fresh water, extending the zone of damage further down the reef slope on the stream-facing side, resulting in more coral destruction here than elsewhere in Kaneohe Bay. The coral communities on the opposite side of the patch reef were seriously damaged only in the upper 2 m (Maragos 1972). The initial phase of recovery of this reef slope was monitored from 1968 to 1973 (Maragos 1974). In July 1983, the Kahaluu reef slope was resurveyed at 10 transect sites replicating the earlier investigation.

MATERIALS AND METHODS

The coral communities of Kahaluu patch reef were resurveyed at 10 stations evenly spaced along the southern and western (stream-facing) slopes of the reef, closely approximating the sites used in earlier studies (Figure 1). The stations were positioned perpendicular to the reef slope at progressively greater distances from the coral areas less damaged by the 1965 flood. Stations 1 and 10 were positioned on undamaged corals and were within 5 m of the damaged/undamaged reef boundary while stations 5 and 6 were over 100 m from the boundary. At each station, data on coral colony size, species composition, and number of species were obtained using the methods of Maragos (1974). A frame (1 m^2) was positioned on the reef flat at the upper slope edge. Water depth varied from 0.5 to 1.0 m. The maximum diameter and species of each coral colony lying at least 50% within the quadrat were recorded. The frame was then moved down the slope in a series of consecutive units 1 m^2. The slope angle varied from 30 to 90° from the horizontal but was predominantly within the 45 to 60° range. Information was gathered in each successive quadrat until no corals were encountered or observed beyond the last quadrat along the transect line. Thus, a transect 1 m wide beginning at the top of the patch reef slope and extending a distance of 6 to 10 m down slope was surveyed at each station. Water depths at the base of the patch reef varied from 4 to 6 m.

In quadrats of high coral cover, colonies may make contact and sometimes fuse together, forming aggregate coral heads of irregular shape. Discernable discontinuities in color and morphological features enabled individual colonies to be distinguished and counted separately. A few larger colonies had dead central and upper portions. These were measured as whole live colonies unless highly fragmented, in which case the distinct live portions were measured separately.

The 1983 resurvey and the earlier survey by Maragos (1974) provided comparative data on the size, abundance, and distribution of corals on the patch reef 8 and 18 yr after the freshwater kill. Species composition was examined in terms of total numbers of colonies and total areal coverage of each colony of each species. Colony diameters were converted to areal coverage using the formula: area = 3.14 r^2, where r = 1/2 the measured

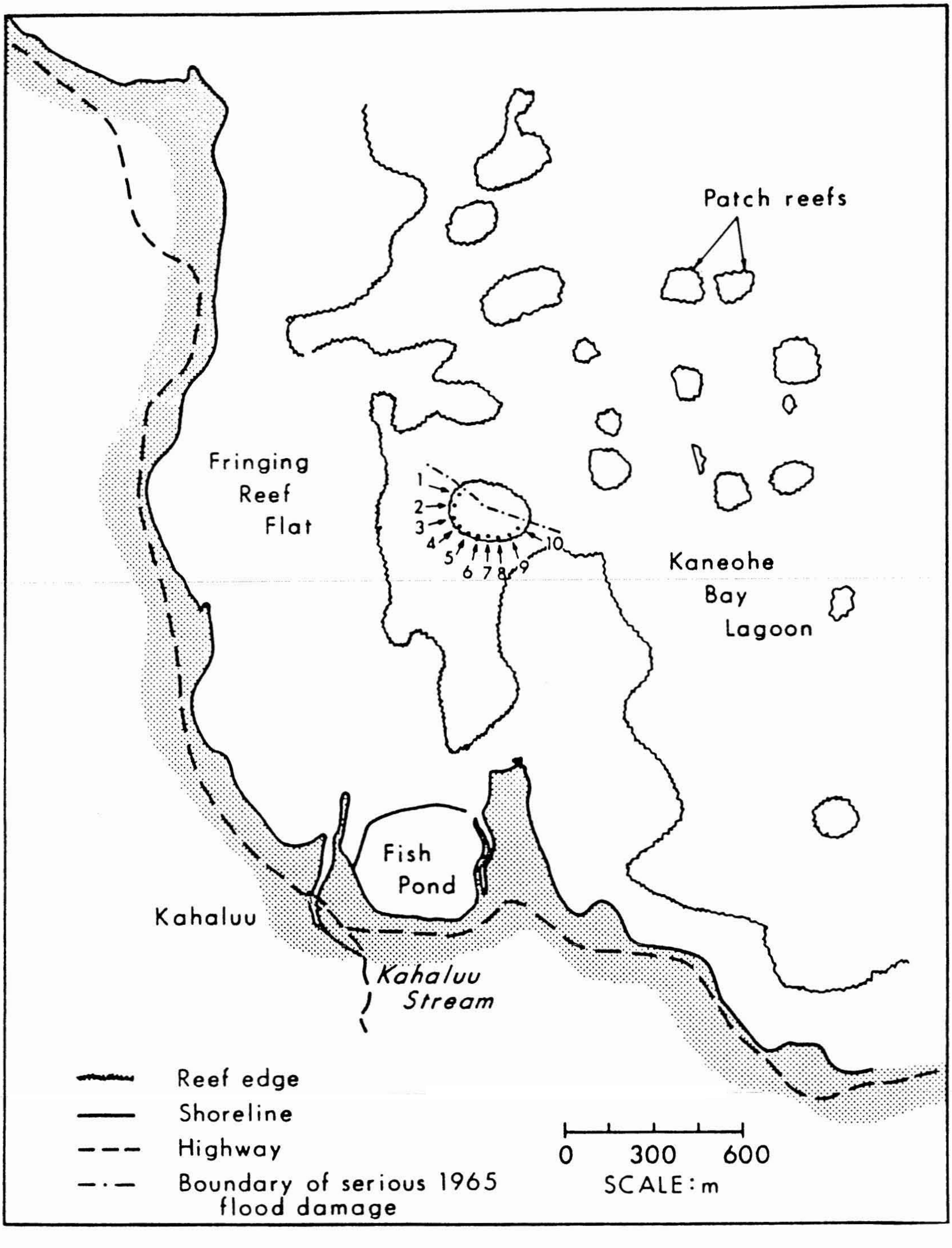

FIGURE 1. Location of the patch reef near Kahaluu Stream with position of 10 transect stations surveyed in 1973 (forty-six 1-m^2 quadrats) and 1983 (eighty-one 1-m^2 quadrats) (after Maragos 1974).

diameter. Because coral colonies are multidimensional forms that often overlap, areal coverage was calculated in absolute amounts of coral cover. From this information, the mean percentage cover of each species per 1-m^2 quadrat was calculated. The mean number of coral colonies of each species per quadrat and the mean colony size of each species were also determined.

Coral distribution was analyzed both as a function of distance from the surviving coral community and depth. Horizontal zonation was examined in numbers of colonies and total coral areal coverage at each transect station. Vertical zonation was plotted both as the number of colonies and total coral area coverage per quadrat along each transect down the reef slope. Coral community diversity was measured for the 1973 and 1983 Kahaluu reef coral assemblages and compared using the Shannon-Wiener Index (Pielou 1966).

RESULTS

On the Kahaluu patch reef between 1973 and 1983, coral abundance increased in terms of colony numbers, areal coverage, and colony size (Table 1). Overall coral coverage increased by 660% while the total numbers of colonies increased by about 150%. However, large variations occurred between quadrats in the amount of coral coverage, number of colonies, and size of colonies, as evidenced by the standard deviations (Table 1). The same four coral species reported in 1973 [*Porites compressa* Dana, *Montipora verrucosa* (Lamarck), *Pocillopora damicornis* (Linnaeus), and *Cyphastrea ocellina* (Dana)] contributed nearly all of the coverage and colonies encountered in 1983. Two additional species (*Porites lichen* Dana and *Montipora patula* Verrill) were reported in 1983, but were minor constituents.

Porites compressa and *Montipora verrucosa* together composed 96.5% of the total coral cover in 1973 and 97.5% in 1983. *P. compressa* alone accounted for 86.3% and 87.9% of coral coverage in 1973 and 1983, respectively. In contrast to the relatively constant proportion of areal coverage by *P. compressa*, its mean coverage per 1-m^2 quadrat nearly quadrupled from 11.28% in 1973 to 43.59% in 1983 (Table 1). During that same period, the mean number of *P. compressa* colonies per quadrat declined slightly (7.56 in 1973 versus 6.44 in 1983) while mean colony size almost doubled (Table 1). Data on size frequency distribution illustrate this shift toward greater numbers of larger colonies for *P. compressa*, as well as for *M. verrucosa* and *Pocillopora damicornis* (Figure 2). In 1973, no colonies greater than 30 cm in diameter were reported. By 1983, over 25% of all measured colonies were larger than that size.

There was no distinct pattern of coral recolonization in relation to distance from the less-damaged reef community on the opposite side of the patch reef (Table 2). Vertically on the patch reef slope, high coral coverage and colony numbers occurred in the upper five 1-m quadrats in 1973. By 1983, the zone of high coral coverage had extended downslope somewhat, although the total numbers of colonies had not increased much (Figures 3, 4). The total depth range of corals along the reef slope nearly doubled by 1983.

Porites compressa thus showed a substantial increase in substrate coverage, mean percentage cover per quadrat, number of colonies, and mean colony size between 1973 and 1983 (Table 1). At the same time, the mean number of coral colonies per quadrat, including *P. compressa*, decreased, indicating a shift in coral community composition. The greater dominance of *P. compressa* is manifested in a slight decline in community diversity between 1973 and 1983, from 0.50 to 0.45, respectively, on the Shannon-Wiener Index of community diversity. Although the decrease is not striking, the results show that diversity has not increased in the 10 yr between surveys.

DISCUSSION

Kahaluu patch reef is similar in structure to other patch reefs in Kaneohe Bay (Maragos 1972, Evans et al. 1986, Holthus 1986). The seaward side of Kahaluu patch reef, which was not extensively affected by the freshwater runoff event of 1965, is similar in its species

TABLE 1

SUMMARY OF THE TRANSECT DATA* FOR THE 1973 AND 1983 SURVEYS

CORAL SPECIES	CORAL COVER: TOTAL CORAL COVER (m^2)	CORAL COVER: % OF TOTAL	CORAL COVER: MEAN % COVER/ QUADRAT	CORAL COVER: S.D.	NUMBER OF COLONIES: TOTAL NO. COLONIES	NUMBER OF COLONIES: % OF TOTAL	NUMBER OF COLONIES: MEAN NO./ QUADRAT	NUMBER OF COLONIES: S.D.	COLONY SIZE: MEAN DIAMETER (cm)	COLONY SIZE: S.D.
1983										
Porites compressa	3,580.66	87.9	43.59	37.28	522	75.0	6.44	5.09	25.23	15.14
Montipora verrucosa	391.16	9.6	4.84	13.19	59	8.5	0.73	1.35	20.38	17.74
Pocillopora damicornis	39.33	1.0	0.49	1.77	67	9.6	0.86	1.79	6.90	8.09
Cyphastrea ocellina	3.93	0.1	0.05	0.15	43	6.2	0.53	1.56	8.05	8.17
Montipora patula + *Porites lichen*	57.95	1.4	0.72	4.71	5	0.7	0.06	0.29	31.50	33.73
Total	4,073.03	100.0	50.31	—	696	100.0	8.62	—	—	—
1973										
Porites compressa	528.82	86.3	11.28	12.70	348	73.0	7.56	5.27	12.66	15.48
Montipora verrucosa	62.59	10.2	1.36	2.78	53	11.1	1.15	2.07	10.94	6.18
Pocillopora damicornis	19.63	3.2	0.43	0.83	70	14.7	1.52	1.47	11.61	11.32
Cyphastrea ocellina	1.52	0.3	0.03	0.15	6	1.2	0.13	0.40	5.17	2.56
Total	612.56	100.0	13.10	—	477	100.0	10.36	—	—	—

*Total number of transects surveyed: 1973 = 46, 1983 = 81.

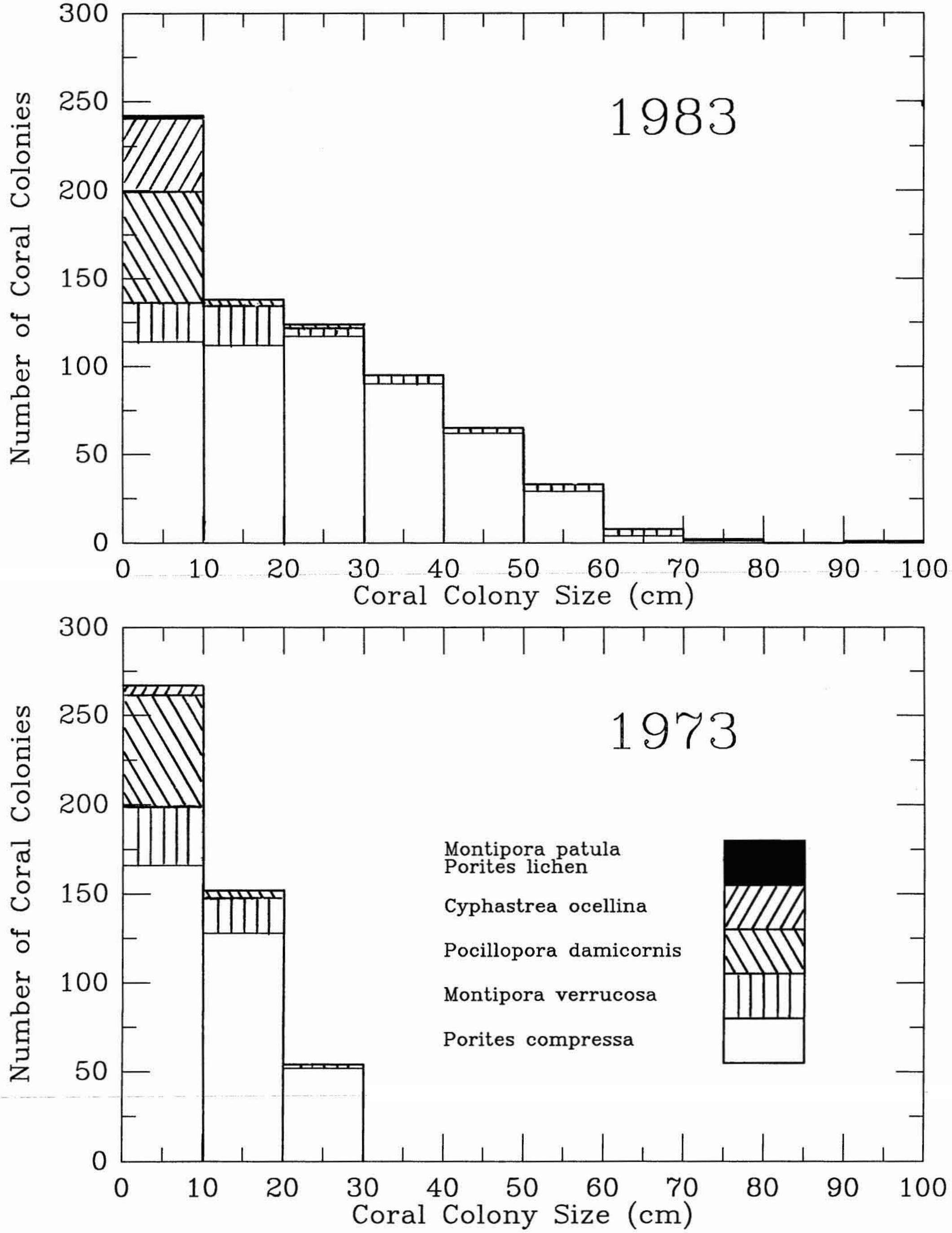

FIGURE 2. Size frequency distribution for combined transect data, showing number of coral colonies (n) for each size class in 1973 ($n = 477$) and 1983 ($n = 696$).

TABLE 2

HORIZONTAL ZONATION: NUMBER OF CORAL COLONIES AND CORAL COVER (m^2), IN ALL QUADRATS AT EACH STATION, AND CHANGE BETWEEN 1973 AND 1983

	SURVEY STATION									
	1	2	3	4	5	6	7	8	9	10
CORAL COVER (m^2)										
1983	268.77	156.77	170.2	208.44	246.25	253.64	170.49	212.68	241.42	135.26
1973	33.31	24.74	35.25	38.25	34.01	24.78	25.76	25.53	40.39	24.23
Change	+235.46	+132.03	+134.95	+170.19	+212.24	+228.86	+144.73	+187.15	+201.03	+111.03
% Change*	807	634	483	545	724	1024	662	833	531	558
NUMBER OF COLONIES										
1983	64	77	44	98	67	88	45	74	64	71
1973	78	58	57	55	56	32	30	24	51	36
Change	−14	+19	−13	+43	+11	+56	+15	+50	+13	+35
% Change*	82	133	77	178	120	275	150	308	125	197

* % change calculated as 1983/1973 × 100.

composition and level of coral coverage to patch reef communities elsewhere in central Kaneohe Bay (Maragos 1972, Evans et al. 1986). The reefs in central Kaneohe Bay have been subject to similar levels of stress from sewage pollution and runoff from suburban development (Smith et al. 1973, Banner 1974) and are shown to be recovering from those effects in a similar manner (Maragos et al. 1985, Evans et al. 1986).

It is thus reasonable to assume that, from 1965 to 1983, Kahaluu patch reef had not been subject to influences different from those affecting other reefs in the area. The recovery of the Kahaluu coral community is thus proceeding in response to the coral recruitment and coral community succession processes typically operating in Kaneohe Bay.

Coral Recruitment

Because no living coral survived on the landward reef side, the recolonization of Kahaluu patch reef was dependent upon the dispersal and recruitment of planktonic coral larvae from the opposite side of the reef or from elsewhere in the bay. Colonizing corals on the denuded reef front did not show a trend of increasing or decreasing frequency in relation to increasing or decreasing distance from reef coral communities on the seaward side of Kahaluu patch reef that survived the 1965 flood (Table 2). Hence the data do not suggest higher rates of recruitment from the nearest source of coral larvae (i.e., the surviving coral communities on the opposite site of the same patch reef). Fitzhardinge (1985) showed that coral recruitment is not linked to the abundance of adult colonies nearby and that the overall abundance of *Porites compressa* in Kaneohe Bay (Maragos 1972) was not reflected in increased recruitment of that species.

Large numbers of planktonic coral planula are produced on reefs in Kaneohe Bay and transported between reefs within the bay (Hodgson 1985). However, coral recruitment within Kaneohe Bay is highly variable, both spatially and temporally, probably because of differences between reefs in larval production and dispersal (Hodgson 1985), grazing, and the composition of substrate epiflora and

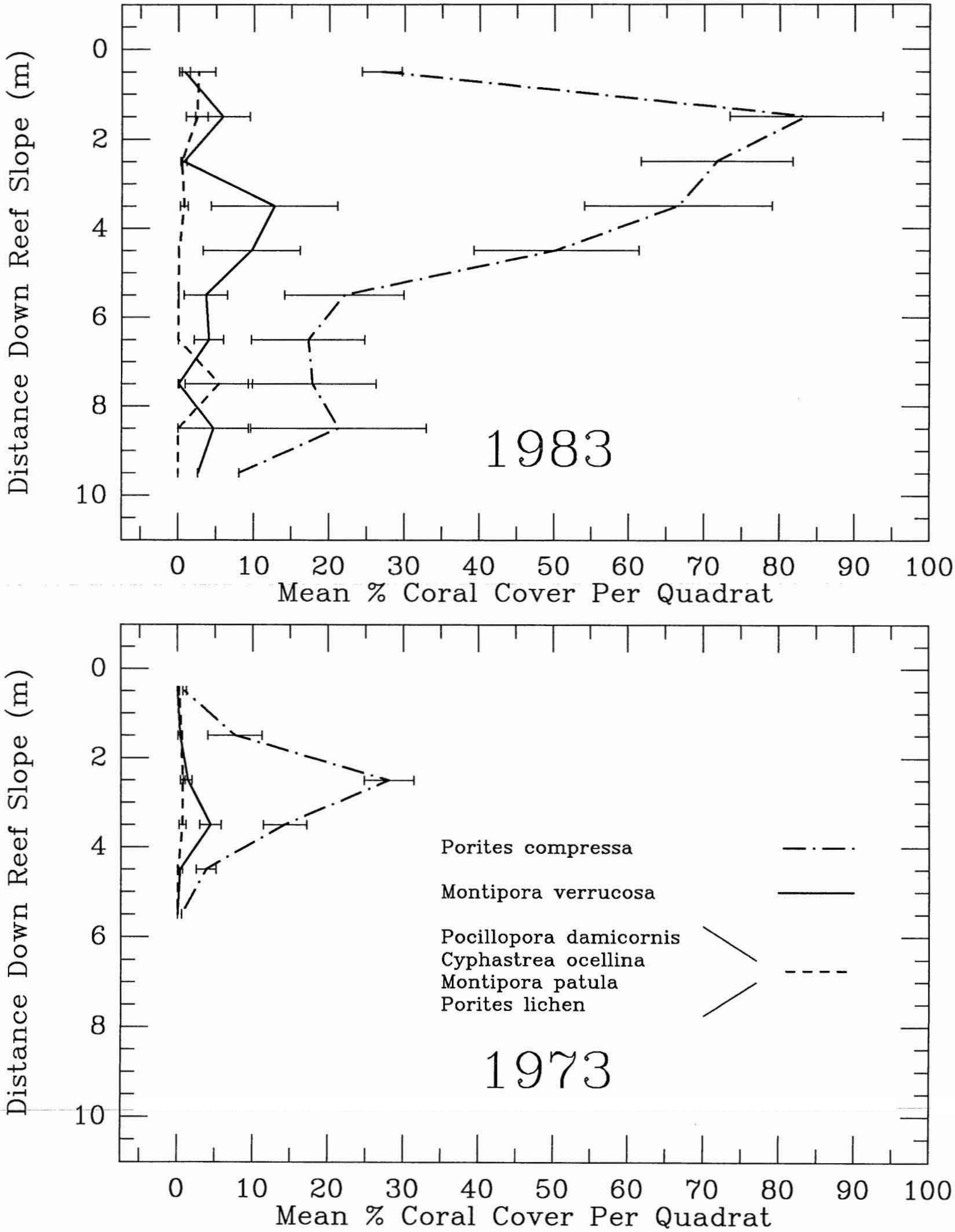

FIGURE 3. Vertical zonation: mean percentage coral cover per m² down reef slope. Number of quadrats at each distance down reef slope (1, 2, 3, etc.) was 10, 10, 10, 10, 10, 10, 9, 7, 4, 1, respectively, for 1983 and 10, 10, 10, 10, 5, 1, respectively, for 1973. Total number of quadrats: 1983 = 81, 1973 = 46.

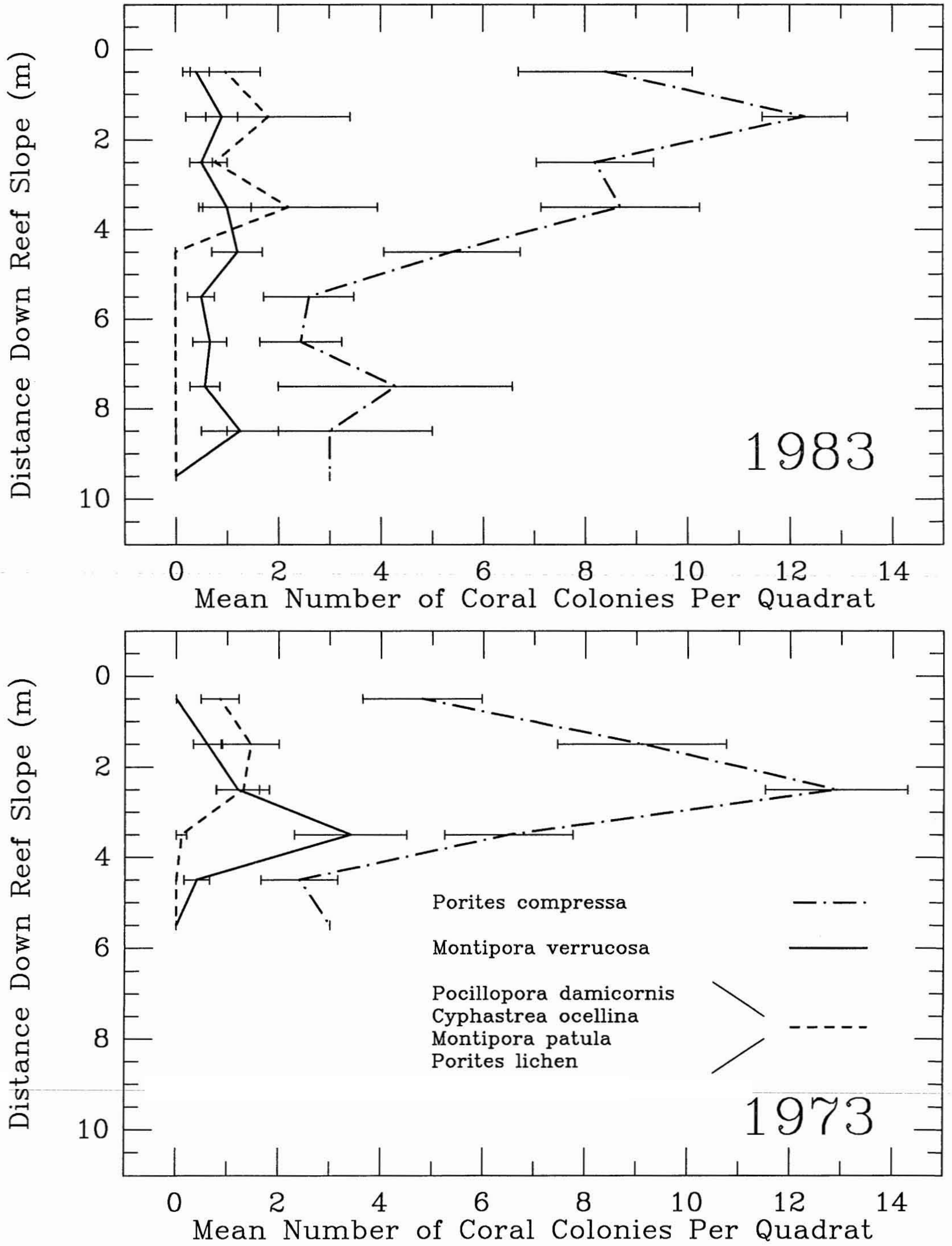

FIGURE 4. Vertical zonation: mean number of coral colonies per quadrat down reef slope.

epifauna (Fitzhardinge 1985). The recolonization of the Kahaluu patch reef was thus probably initiated with mixed recruitment of planktonic coral planula of the common species found in the Kaneohe Bay lagoon.

Patterns of Succession in Hawaii

Patterns of coral succession on Hawaiian reefs were first described by Grigg and Maragos (1974), who assessed coral communities that had colonized submerged lava flows. Community composition, distribution, and structure were measured on a series of known-age lava substrates 10 to 100 yr old and on adjacent reference reefs on the island of Hawaii. The number of coral species present, density, percentage cover, and diversity were studied in relation to age of substrate and degree of exposure to sea and swell at each station. At the most sheltered stations, Grigg and Maragos (1974) found that coral cover was high and the amount of cover was negatively related to wave exposure. In addition, where coral cover was high, diversity was low, indicating dominance by one or two species. The total number of species present per station was relatively constant.

In less exposed areas, where physical processes were not constantly interrupting succession, diversity rose initially as all coral species colonized the available substrate. As space became limiting and interspecific interactions increased, the competitively successful species (especially *Porites lobata* Dana and *Porites compressa*) became dominant and diversity decreased. Grigg and Maragos (1974) estimated that complete recovery of reef coral communities on lava flows off the island of Hawaii may occur within 15 to >50 yr depending on degree of exposure, with climax achieved more quickly in exposed environments.

In a detailed 11-yr study on the island of Hawaii, Maragos (1983) followed the development of coral communities at Honokohau Harbor after it was quarried from sterile basalts inland from the shoreline and opened to the sea in 1970. Successional patterns similar to those on the "natural" lava flows were encountered in the protected harbor environment, which was determined to be very favorable for coral colonization and growth. The coral community developed more rapidly in the outer harbor than on the flows as a result of the greater protection from wave exposure and the stability and suitability of the substrate. The mean frequency of coral colonies per meter square unit area reached a plateau after 6 yr. Coral abundance, as estimated from percentage coverage, however, continued to rise 11 yr after harbor construction. An encrusting species, *Porites lobata*, became more and more dominant over time. Corresponding with the increasing dominance of *Porites lobata*, coral community diversity decreased following a peak 7 yr after the harbor was available for coral recruitment.

Coral Community succession in Hawaii: Kahaluu Patch Reef

In an overview of coral reef community structure and succession in Hawaii, Grigg (1983) suggested that most differences in community structure are those related to species adaptations. The species that eventually dominate coral communities in Hawaii are usually either the most tolerant to wave stress (*Porites lobata*) or competitively superior (*Porites compressa*). Grigg (1983) concluded that the primary mechanism controlling diversity, community structure (dominance and patchy distribution of coral species), and succession of coral reefs in Hawaii is disturbance. On exposed coasts, which dominate reef habitats in Hawaii, long period swell and wave action are the major sources of physical disturbance (Dollar 1982), while in protected environments a lack of disturbance may be equally or more important. In areas sheltered from wave disturbance, such as Kaneohe Bay lagoon, coral communities can develop to a level at which control is exerted by biological factors (e.g., competition for space) or less frequent physical disturbances (e.g., major floods).

The relatively small number of coral genera present in the Hawaiian Islands and the low number of species within genera facilitate the study of reef recolonization and recovery. Of the approximately 45 species of hermatypic corals identified in the Hawaiian Archipelago (Maragos 1977, Grigg 1983; Maragos, personal communication), 30 species have been recorded in Kaneohe Bay. Half of these corals are commonly distributed on lagoon reefs in the bay, although community composition is dominated by *Porites compressa* (Maragos 1972). *Porites lobata* is not abundant inside the bay and is confined to outer Kaneohe Bay reefs, which are subject to higher levels of wave energy (Maragos 1972).

At Kahaluu, in the protected central sector of the Kaneohe Bay lagoon, coral community succession proceeds uninterrupted by wave disturbance. The amount of coral cover continues to increase while the number of colonies per unit area decreases with time until a biologically controlled climax community is achieved. Competitively superior *Porites compressa* assumes an increasing dominance of the reef slope community as diversity gradually decreases. However, the fragile colony form of *P. compressa* renders it less suited to the rigorous shallow water conditions characterizing exposed reefs in Hawaii. Consequently, *Porites lobata* and, possibly, *Pocillopora meandrina* Dana are instead the dominant forms in those environments.

In the lava flow and Honokohau studies, the low coral community diversity of early stages rises rapidly to an intermediate peak as more species become established. Although the present study at Kahaluu reveals the increased dominance of *Porites compressa* and nearly the same community diversity index values after 18 yr, a pattern of intermediate higher diversity cannot be determined because only two surveys, 10 yr apart, were conducted.

The overall pattern of coral community succession at Kahaluu does seem to follow that proposed for Hawaiian coral reefs (Grigg and Maragos 1974, Grigg 1983). Results from previous surveys in Kaneohe Bay by Maragos (1974) indicate that protected environmental conditions and other factors may result in complete reef slope recolonization within 30 yr. The present study shows that, 18 yr after destruction, the coral community on Kahaluu patch reef is proceeding rapidly in a pattern of succession suggested by previous investigations in Hawaii. However, the pattern of coral reef succession in subtropical Hawaii may not hold for reef environments with a greater diversity of coral species and habitat.

ACKNOWLEDGMENTS

We thank the staff of the summer course for their assistance. Special thanks are given to P. Jokiel for support and encouragement, to P. Aliño for field assistance, and to M. McGinn for assistance with statistical analysis and graphics.

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